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Basic Patterns of Display in Fiddler Crabs (Ocypodidae, Genus *Uca*) [1,2]

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(Plate I; Text-figures 1-4)

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I. INTRODUCTION

THIS contribution is a preliminary result of a general study of ocypodid crabs. The elaborate and varied displays characteristic of the fiddler crabs (genus *Uca*) appear to contribute substantially to an understanding of the phylogeny of the group. An interim report is presented because the increasing use of fiddler crabs in biological research makes their relationships of timely interest.

Specific differences in display behavior were described in an earlier study (Crane, 1941) where it was found that in a group of sympatric species of *Uca* on the west coast of Central America every species could be distinguished from every other species by the form of the display. Even species which could not be otherwise distinguished without a lens were easily identified at a distance by the characteristic form and tempo of the "waving" of the large cheliped. It was found further that closely related species had similar types of display which were divisible into a number of groups.

During subsequent years other American species of *Uca* have been studied in the field on both sides of the continent, from California to Guayaquil, Ecuador, and from Massachusetts to Rio de Janeiro, Brazil (Crane, 1943, 1944 and unpublished).

Now, through a grant from the National Science Foundation, the work has been expanded into a world-wide program. In 1955 and 1956 the crabs were studied in Pakistan, Ceylon, Malaya, Singapore, Sarawak, the Philippines, north and northeast Australia, Fiji, Samoa, Tahiti and adjacent islands. Early in 1957 Panama was revisited, and previously known species reviewed in the light of the recent studies of Indo-Pacific forms. The behavior of the crabs, particularly of displaying individuals, was recorded in color on more than 9,000 feet of 16 mm. motion picture film. This material, along with the correlated and supplementary field notes, forms a permanent record for comparative laboratory analysis. The displays of about 19 good Indo-Pacific species of *Uca* have been recorded in this manner and 29 American forms. Although extensive field work remains to be done, particularly in Africa, the principal outlines of the development of display in the group appear now to be clear.

All detailed supporting data, discussion on the functions and releasing mechanisms of display, specific correlation of display with morphology and discussion of display in relation to infraspecific categories and speciation are reserved for a monographic report on the genus, now in preparation. The following subjects more or less closely associated with display will also be treated only in the later publication: color change, sound

[1] This study has been supported by a grant from the National Science Foundation.

[2] Contribution No. 975, Department of Tropical Research, New York Zoological Society.

production, territoriality, physical combat between males and the erection of structures near the burrows.

Among the many people who have facilitated the field work I wish at this time to express my appreciation particularly to Dr. William Beebe, Director Emeritus of the Department of Tropical Research, New York Zoological Society, and to Dr. Waldo L. Schmitt, Chief Curator of Zoology at the United States National Museum. Both were instrumental in inaugurating the study and, through the years, have given most helpful advice and encouragement.

II. General Form of Display in Fiddler Crabs

The outstanding characteristic of displaying fiddler crabs is a rhythmic elevation and lowering of the hypertrophied major cheliped of the male. In the few species usually familiar to western observers in the field this takes the form of "waving" or "beckoning," and is characteristic of the breeding season. The significance of the gesture has been described by various workers as non-sexually territorial, sexually territorial, a sex attractant, a challenge to other males and as various combinations of all of these possibilities. Although it is not proposed at this time to contribute further to the discussion, it may be said that field observations and motion picture records prove conclusively two points. First, all the suggested functions occur, sometimes all in a single species. Furthermore, in some advanced species there are distinct differences separating territorial, male-to-male and male-to-female displays, the latter being the most highly developed.

The motion of the cheliped is by no means always wavelike; in some species it is the merest slight raising of the flexed manus and chelae in front of the buccal region. In others it is a violent, very rapid shaking of the same parts at the level of the eye-stalks; in others the base of the manus is rapped against the ground, the waving is in jerks, or the cheliped is held high and revolved in circles. Among these extremes there are all degrees. Tempo is exceedingly various and specific, although unrelated crabs often wave at about the same rate of speed. Single waves range from one wave lasting 13 seconds to five waves being crowded into a single second. The first extreme of timing is found in certain South American populations of *U. pugnax rapax* under certain conditions and the second in an apparently undescribed species from Port Darwin, Australia. The waving rate of most species falls between one-half and two seconds per wave.

Motions associated with waving include elevation of the carapace on the ambulatories, revolving, moving from side to side, and various "bounces" and "curtsies" accomplished by rapidly lowering and raising the body on one or both sides.

In the following pages the display motion of the large cheliped will for convenience be termed "wave," whether or not it bears an anthropomorphic resemblance to such a gesture.

III. Basic Wave Patterns

Most of the species of *Uca* may be clearly divided into two groups depending on a basic difference in the direction of the first part of the motion of the major cheliped. These two behavioral complexes are characteristic of the majority of species in, respectively, the "narrow-fronted" and "broad-fronted" groups, as they have been termed in most systematic treatments.[3]

[3] Bott, 1954, basing his decision on a collection of specialized Central American species of *Uca*, gave the narrow-fronted and broad-fronted groups each generic standing, reserving *Uca* for the narrow-fronts and proposing *Minuca* for the broad-fronts. Peters (1955), working on ecological and behavioral aspects of the same material, reduced *Minuca* to subgeneric rank. The present writer currently feels that *Minuca* should be given at most subgeneric status. This view is dependent on the extensive series of intermediate species distributed in other parts of the world, and on the distinctness and homogeneity of *Uca, sensu lata*, in comparison with all other genera in the family. Until further comparative morphological work is completed, it seems preferable to use simply the non-technical terms, "narrow-fronts" and "broad-fronts," as a practical division which for the majority of species appears to be phylogenetically justified.

Vertical Waves. (Text-figs. 1; 4, A-B). In the great majority of narrow-fronts, the cheliped at the beginning of the wave remains flexed in front of the buccal region and is raised up and slightly forward from there, without unflexing, until it reaches the level of the eyeballs. In the simplest displays it reaches no farther and therefore is never unflexed. In more advanced displays its elevation continues obliquely above the eyes, through the unflexing of the manus and chelae. Regardless of the amount of elevation or degree of unflexing, the cheliped is lowered back into rest position in the same plane in which it was elevated. This type of display will be called a "vertical wave."

Lateral Waves. (Text-figs. 3; 4, D-F). By contrast, the characteristic wave form of almost all species of broad-fronted *Uca* commences with a sweep to the side, rather than with a vertical elevation of the cheliped; this kind of gesture will be called a "lateral wave." In moderately intensive display, in which differences among species are most apparent, the flexed cheliped is pushed away from the body at the beginning

of the wave and more or less unflexed toward the side; it then sweeps up to a completely unflexed, high-reaching position. Finally it is flexed once more in front of the buccal region. Since it is often lowered in a direct path, close to the body, a more or less circular motion is completed. The amount of deviation from the path of the first part of the wave differs among species, and within species depending on the degree of display intensity; therefore the circularity varies widely; sometimes, in fact, lateral displays are altogether single plane. In displays of the lowest intensity of all, even laterality is often absent, the cheliped motion closely resembling the slight, flexed, single-plane display of the vertically waving narrow-fronts, as described in the preceding paragraph (Text-fig. 4 C).

Intermediate Waves. The waving pattern of a few species is intermediate between vertical and lateral types. Morphologically these forms also show some characters intermediate between those of narrow-fronts and broad-fronts.

Position of Body during Waving. In addition to the form of the wave there are several fundamental differences in the position of the body during waving. In some species it is scarcely raised at all; in many it is raised on the ambulatorics and lowered with every wave; in still others it is raised and held erect during a series of waves. The amount of elevation varies somewhat within species in accordance with the intensity of waving.

Systematic Distribution of Basic Wave Patterns. An arrangement of species characterized by various types of wave is presented in Table 2. Authorities for the species, geographical distributions and localities where display has been observed are listed in Table I.

As will be seen from Table 2, the vertical type of wave is typical of Indo-Pacific narrow-fronts. These species in turn include those forms in which *Uca* display is simplest and, it seems unquestionably, most primitive. These uncomplicated displays are found in *manii, rhizophorae* (Text-fig. 1, A-B), *rosea, ischnodactyla* and *rathbunae;* in these species the body is scarcely if at all raised above the ground during display. *U. dussumieri* is somewhat further advanced. Although specific differences in the waving pattern of all of these are clear-cut, the group similarity is obvious to the observer. In all of these species the cheliped is not raised high overhead, and the amount of time devoted to waving is negligible in comparison with that so spent in the more advanced species.

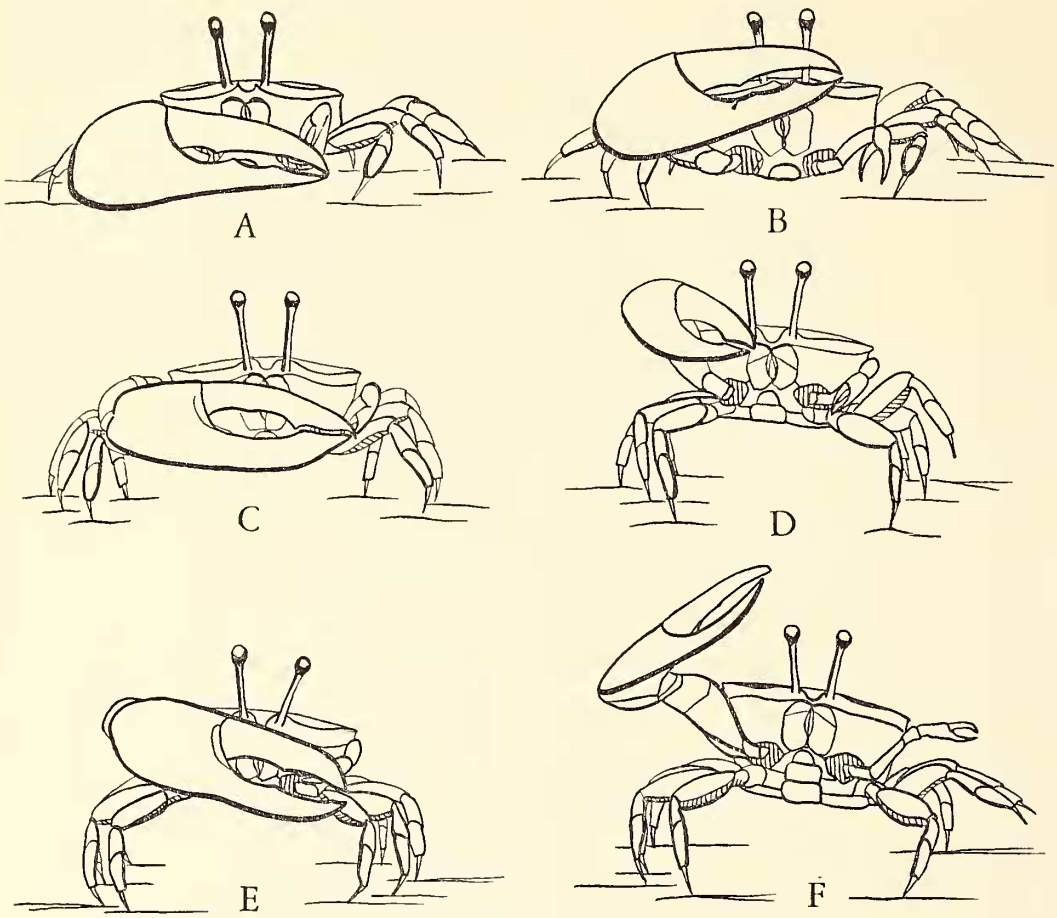
The waving of still other narrow-fronts from the Indo-Pacific is considerably more advanced, as in *marionis, signata* (Text-fig. 1, C-D) and *zamboangana* (Text-fig. 1, E-F). Although the pattern is still vertical and single plane rather than lateral in character, the reach is higher, the tempo tends to be swifter, the proportion of time devoted to waving greater and the elevation of the body conspicuous.

Neotropical members of the narrow-fronted group are aberrant as well as intermediate, both morphologically and behavioristically. The display is characterized by a lateral, not vertical, type of wave. Except in low intensity display the gesture is spiral, rather than merely circular, since the cheliped, after its initial lateral elevation, is revolved throughout a series of waves without being lowered to the ground. This lateral, spirally circular display has been observed in *heteropleura, heterochelos, stylifera, princeps, maracoani* and *insignis* (Text-fig. 2). It reaches its maximum development in the two latter species, which are allopatric counterparts in the Atlantic and Pacific. In both of them, which attain large size and a correlated remarkable development of the heterogonic major cheliped, the chelae are directed upward, spread wide apart and then rotated without pause, often for several minutes at a time. Even in their low intensity displays these two species are of the lateral type; in the others, however, low intensity waving shows single-plane, vertical-wave affinities. Most of the group hold the carapace high during a series of waves, although in *stylifera* and *princeps* the hind legs bend during the highest reach of the cheliped, tilting the posterior part of the carapace downward. *U. heteropleura, heterochelos* and young *princeps* raise and lower the carapace with each wave.

Two narrow-fronted crabs, the Australian *longidigitum* and the Indo-Pacific *tetragonon,* as well as the Indo-Pacific broad-fronted *gaimardi,* all show wave characteristics intermediate between the vertical and lateral types. The displays are very distinct, however, and the three species are not morphologically closely related to one another.

Alone among the known displays of broad-fronted crabs the neotropical Atlantic *thayeri* has a vertical, single-plane type of wave similar to those of the Indo-Pacific narrow-fronts. Morphologically, also, *thayeri* shows affinities with those species.

The remaining broad-fronts, in which display has been observed, are all characterized by a strongly lateral type of wave, usually with a variable degree of circularity (Text-fig. 3). In a number of the very rapidly waving neotropical broad-fronts, such as *beebei* and *saltitanta,* the last half of the wave is so swift that the eye does not record it. Hence although the motion was often described in field notes as a single-plane wave, subsequent examination of



TEXT-FIG. 1. Examples of vertical types of wave in three species of narrow-fronted *Uca* from the Indo-Pacific region. Illustrations on left show rest positions between waves, those on right the maximum elevation of the cheliped, which is raised and lowered in a single plane. Note in the series, reading from the top down, the progressively higher reach of the cheliped and greater elevation of the carapace. See text, p. 70 ff., Table 2 and Text-fig. 4, A-B.

A, B, *U. rhizophorae* (photographed in Singapore); C, D, *signata* (Philippine Is.); E, F, *zamboangana* (Philippine Is.). Drawings by Dorothy F. Warren, after motion picture frames and mounted specimens.

motion picture frames proved that circularity was clearly evident.

Examples of a strongly circular type of lateral wave include the Indo-Pacific *annulipes* and *lactea* (Text-fig. 3, A-D) and the eastern Pacific *latimanus*.

In a few species, such as *U. terpsichores*, the rest position of the cheliped during display is with the chelae directed forward.

An aberrant group of broad-fronts, of which *pugnax rapax* (Text-fig. 3, E-F) is typical, is an important element in neotropical *Uca;* two Atlantic representatives extend even into the north temperate region (*pugnax, minax*). They are all characterized by exceedingly broad fronts and by a jerking, obliquely-lateral wave which during moderate intensity is circular. They have no Indo-Pacific representatives.

The lateral wave of the broad-fronts, in the progressively specialized species, shows increasing speed, maximum unflexing of the cheliped and more prolonged periods of time devoted to waving.

It has already been noted that in species in which waving is poorly developed (*rhizophorae, manii,* etc.) the body is raised scarcely or not at all during waving. In the majority of species, among both narrow-fronts and less advanced broad-fronts, the carapace is raised on the ambulatories and lowered with every wave. In some

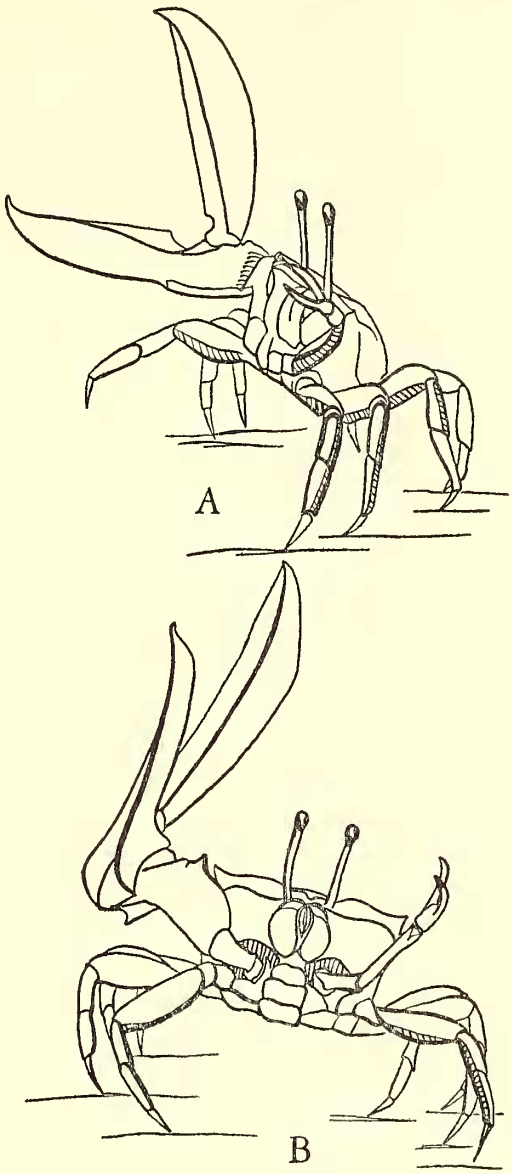
lateral wavers, the body is only slightly elevated, but is held in this position throughout the series. (In a few of this group, for example in *beebei,* an impression of raising-and-lowering is given by the tendency of the crab to bend the hind legs during the peak of the cheliped reach, thus tilting the carapace down posteriorly; this is especially true when the crab is displaying on soft mud; c.f. Peters, 1955, who reported that this form raises and lowers the carapace with every wave). In advanced species among both narrow-fronts and broad-fronts, the body is held high on the ambulatories throughout a series of waves.

IV. Advanced Stages of Display

One behavioral distinction between the narrow-fronts and the broad-fronts is found in all the species so far observed except for a few instances. This concerns the final stages of premating behavior.

Advanced Display in Narrow-fronts. In the narrow-fronts the male pursues a female or approaches her at the mouth of her burrow; this behavior does not necessarily immediately follow display, although the male always has been displaying during the same low-tide period. The approach, however, often does follow display directed more or less toward a female, although this individual is not necessarily the one which is eventually approached. There is no marked increase in tempo of waving during the approach, and additional elements of display are lacking, except for a few special steps in the aberrant neotropical *stylifera, insignis* and *maracoani.* When within reach, the male seizes the female and, after brief tapping or stroking of her carapace with his ambulatories, attempts copulation at or near the mouth of her burrow. This has been observed by Altevogt (1955) in *marionis* in India; and by the present author as follows: *marionis* in Fiji, the Philippines, Australia and Singapore; *dussumieri* in the Philippines, Sarawak and Singapore; *manii* in Singapore and Penang; *rathbunae* in the Philippines; two undescribed new species in Australia; *heteropleura, stylifera* and *insignis* in Ecuador and Pacific Panama; and *maracoani* in Trinidad, northern South America and Brazil. Actual copulation was seen in *marionis* (four times), *rhizophorae* (twice), *manii* (twice), *dussumieri* (once), Australian new species (once) and *stylifera* (once). The last stage of courtship, involving stroking, has been observed probably 75 times at a conservative estimate, although these latter episodes did not, after display, end in copulation.

A few instances of apparently atypical behavior is known in the narrow-fronts. Females of *stylifera* (Crane, 1941, p. 172) *insignis* and *signata* were seen on one occasion each to follow a displaying male into his burrow. Two small *princeps* (*ibid,* p. 170) seized females. Each tried unsuccessfully to drag the female down



Text-fig. 2. Lateral circular type of wave in the neotropical crab, *Uca insignis* (photographed in Panama). Carapace is held high on the ambulatories throughout a series of high-reaching circular waves, during which the cheliped is never brought down into the flexed position of rest. **A,** maximum reach of cheliped; **B,** "low" position, between waves. See text, p. 71, and Table 2. Drawings by Dorothy F. Warren after motion picture frames and mounted specimens.

his own burrow, grasping her with the ambulatories of the minor side.

During all of the above instances where I have observed final stages of display and copulation above ground I have never once seen the male seize and hold the female with the major cheliped. Therefore the definite holding observed by Altevogt near Bombay in copulating *marionis* (1955.2, p. 518) apparently is of rather exceptional occurrence.

Advanced Display in Broad-fronts. In the broad-fronted group, in addition to an increased tempo of display at the approach of a female, there are specialized steps, curtsies or rappings which are only elicited at this time.

Another group distinction is apparent at the end of courtship. In the broad-fronts the usual procedure is for the male, after high intensity display, to precede the female down his own burrow; the female may or may not follow, and may or may not stay below, presumably copulating, for any length of time. I have seen the female actually follow the male into the burrow in the Indo-Pacific *annulipes* in Karachi, Singapore, Sarawak and Davao; in *lactea* in Pakistan, Singapore, the Philippines, and Fiji; in the Pacific neotropics in *stenodactyla, beebei, batuenta, saltitanta* and *latimanus*; and, finally, in the western Atlantic in *pugnax, pugnax rapax, pugilator, cumulanta, leptodactyla* and in two apparently undescribed new species.

In only two broad-fronts, *stenodactyla* and *beebei* in Panama, was copulation seen; this was at the surface by the female's burrow as in narrow-fronts (Crane, 1941, pp. 193, 197). A number of females in each of these two species, however, have been seen to follow the male in the usual broad-front fashion. Throughout the broad-fronted group, therefore, underground mating in the male's burrow is presumably the rule and the female, instead of being pursued toward her own burrow by the male and often seized more or less forcibly, is attracted by rapid and characteristic display into the burrow of the male which she enters after he has disappeared.

In the broad-fronted *gaimardi* (= *pulchella* Stimpson) in Tahiti both the first and the last stages of display appear almost perfectly intermediate betwen those typical of the primitive narrow-fronts and of the broad-fronts. The intermediate character of the wave has already been mentioned; advanced stages of display were lacking and the male pursued the female as in narrow-fronted crabs. Even during high intensity display the carapace was scarcely elevated. Morphologically, as usual with crabs having intermediate displays, the species shows intermediate characters.

Another broad-fronted species of particular interest is *saltitanta,* from the Pacific neotropics. As noted previously (1941, p. 166) this form represents the extreme in development of the rapping type of display, which occurs in a number of related species on both coasts of tropical America. In these species a crab, at the end of a wave, may bounce the lower edge of the major manus and pollex on the ground (Text-fig. 4 F). Usually this bouncing or rapping occurs only when the crab is excited, often in the final stages of courtship. It is typical immediately before the male's descent into his own burrow, after display has been directed toward a particular female. In *saltitanta* the rapping has been pushed forward to become an integral part of routine waving, whether or not the crab is particularly excited and whether or not display has been directed toward a female.

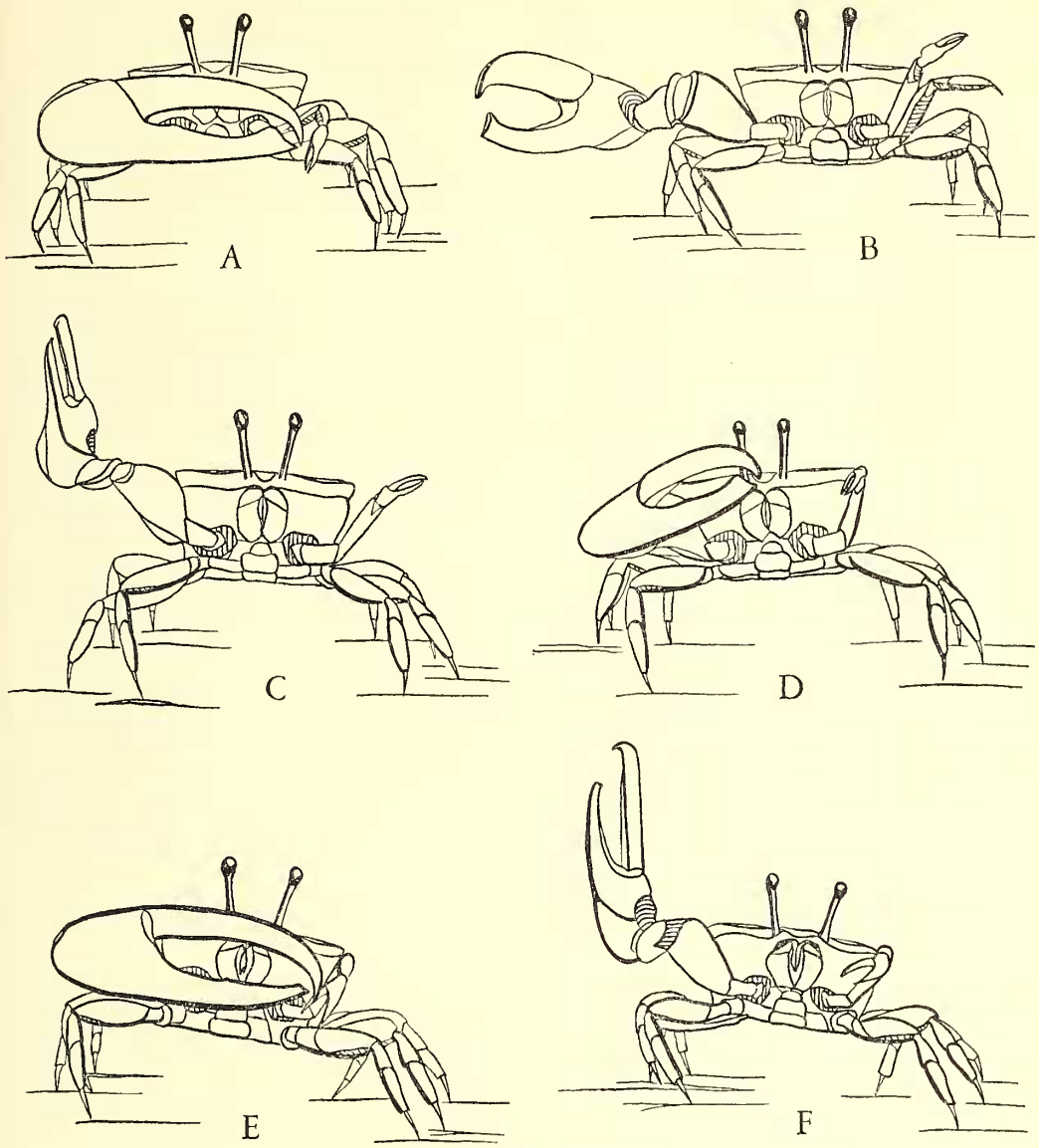
The basic characteristics of the lateral wave itself may be superceded during the specialized motions of advanced display. Depending on the species, the cheliped may be held motionless overhead, or in front, while the crab bobs and races to and fro. Again, the cheliped, having passed through stages of low-intensity single-plane and high-intensity circular display, reverts once more to a single-plane return; now, however, the cheliped is opened laterally and raised to maximum height while the waving tempo is greatly increased. In a number of species the cheliped is not returned to its usual rest position between waves, but performs an aerial circle, somewhat similar to that found in the aberrant neotropical narrow-fronts.

In Table 2 only a slight indication is given of the types of advanced display occurring among the broad-fronts. In spite of group similarities, the display of each species is so distinct that, if seen in moderate intensity and advanced stages, none could ever be confused in the field with that of any other species, even from other parts of the world.

As in studies of the complex displays of certain vertebrates, it is obviously essential, both for accuracy of description and for an approach to understanding, that the displays be observed for prolonged periods and under a variety of conditions.

V. Ecological Differences in the Distribution of Display Types

In 1941 (p. 160) the present investigator noted that the most highly developed displays in western Central American crabs were found in species living on the shores of bays and estuaries which, while protected from waves, were freely confluent with the open sea and consequently of



TEXT-FIG. 3. Examples of lateral types of wave in broad-fronted *Uca.* **A-D,** *U. lactea* (photographed in Fiji Is.), showing maximum development of the lateral circular wave, in which the cheliped starting from the flexed position (A) is unflexed outward (B), then raised (C), and finally returned (D) to the starting point. This wave is best developed in displays of moderate intensity; at low intensity or at high intensity during advanced display, the wave may be of a vertical or lateral single plane type. See text, p. 71, Table 2 and Text-fig. 4, C-E. **E, F,** *U. pugnax rapax* (Venezuela). Rest position and maximum cheliped reach of lateral circular wave, characteristic of moderate intensity display. Cheliped is unflexed outward, raised and lowered in a series of jerks. See text, p. 72, and Table 2. Drawings by Dorothy F. Warren, after motion picture frames and mounted specimens.

relatively high salinity. Recent observations in the Indo-Pacific have shown agreement. In both the narrow-fronted and broad-fronted groups the most actively displaying species, which apparently are also most morphologically advanced, are those in similar localities. Examples of Indo-Pacific crabs with well developed displays are the narrow-fronts *marionis* and *tetragonon* and the broad-fronts *annulipes* and *lactea;* all live typically on rather open shores or inlets of protected bays, as do their neotropical counterparts including *insignis* and *maracoani* among

the narrow-fronts and *stenodactyla, deichmanni, terpsichores, latimanus* and *leptodactyla* among the broad-fronts. Those with the least developed displays, the Indo-Pacific *rhizophorae, manii,* etc. (p. 71), are also those morphologically the least specialized for an amphibious life; all inhabit less saline situations, sometimes living in almost fresh water, on more sheltered mudflats and streambanks.

An interesting point is that the extremely broad-fronted American group, including *pugnax* and *mordax,* has spread into sheltered localities extending even, in *mordax,* far up tropical rivers. The tempo of their displays is slow, as in sheltered, unrelated species in the Indo-Pacific, but it is clearly of the lateral, highly developed broad-fronted type, and the females, as usual in the broad-fronts, are attracted down the burrows of the males.

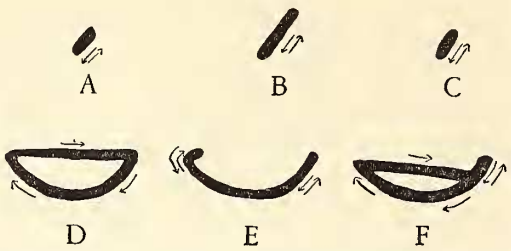
VI. Geographical Distribution in Relation to Display

Those narrow-fronted species with the simplest and apparently most primitive display (*manii,* etc.) are all confined to the Indo-Malayan region, which undoubtedly is the center of distribution for the family. The intermediate narrow-front, *tetragonon,* which currently reaches Tahiti and was formerly found also in Hawaii, shows in its display as in its morphology certain intermediate elements which seem to form a link with the American narrow-fronts. The displays of the latter are more highly evolved than any yet known in the group in the Indo-Pacific, and show affinities to those of the broad-fronts; the species are also specialized morphologically, being characterized for example by extreme narrowness of the front, by unique peculiarities of the spoon-tipped hairs of the second maxilliped, and by male abdominal appendages more similar to those of broad-fronts than of Indo-Pacific narrow-fronts.

The broad-fronted displays are represented by both simple and advanced examples in both hemispheres. There are, however, many more American than Indo-Pacific species, and most of the American species are more specialized in both behavior and morphology than any of the observed Indo-Pacific broad-fronts with the exception of *lactea.*

U. gaimardi, the only Indo-Pacific broad-front reaching as far east as Tahiti, appears to be, as is *tetragonon* among the narrow-fronts, an intermediary between Indo-Pacific narrow-fronts and American broad-fronts.

Three Indo-Pacific species have been observed in display over a horizontal distribution of 5,000 to 8,000 miles. These are *marionis, annulipes* and *lactea.* No gross variations in display behavior have been observed among the various populations within each species, although detailed analyses of motion picture film are expected to show minor distinctions. The one major difference, noted among the populations of *lactea,* was that no "shelters" (Crane, 1941, p. 157) were built by the species even at the height of display in Singapore, the Philippines or Fiji. They were, however, built by about one-fourth of the adult male *lactea* in Karachi, Pakistan, in mid-June.



Text-fig. 4. Ground projection of path of various types of wave in *Uca.* In each path the beginning is at upper right boundary of the black line. In **A, B** and **C,** the length of the line represents the extent of the obliquely forward thrust of the cheliped during its elevation. **A,** *U. rhizophorae,* a low vertical wave, single plane; **B,** *zamboangana,* a high vertical wave, single plane; **C,** *lactea,* a vertical, single plane wave occurring in low intensity display; **D,** same, a lateral circular wave, typical of display of moderate intensity; **E,** same, a lateral, single-plane wave found during advanced stages of display; **F,** *saltitanta,* a lateral circular wave, with straight line marking route as cheliped retraces beginning of path, rapping ground in front of crab as the claw bounces back into rest position. Cf. text, p. 70, and Text-figs. 1 and 3.

These projections were obtained by placing a preserved, flexible specimen of each species on a thick sheet of modelling clay and fastening a needle to the tips of the major chelae with scotch tape in such a way that, regardless of the elevation of the cheliped, the needle cut partially through the modelling clay. Starting from the flexed, rest position the cheliped was then moved as though in natural display, in accordance with motion picture records, the tip of the needle marking the projected path.

VII. Evolutionary Trends

The varying patterns of *Uca* display, from the simplest to the most complex, show a trend prevalent in many branches of the animal kingdom in groups where vision is well developed. In *Uca,* as in numbers of birds, reptiles, fishes, spiders and mantids, for example, it is axiomatic that the display increases the conspicuousness of the animal—regardless of the function of the particular display under consideration.

A primary component of the conspicuousness is usually a temporary or apparent increase in size. In fiddler crabs this increase is attained in three ways; first by a progressively higher reach with the cheliped; second by the broadening of the wave into an expansive lateral gesture replacing a close-to-the-body motion; and, third, by the higher and more prolonged elevation of the body on the increasingly straightened walking legs. In some advanced laterally-waving species, however, the body is not held very high, the walking legs being braced far out at the sides; this position seems to be an aid in balancing. It is probably a necessary stance in these species in which both heterogony and the lateral extension of the cheliped are extreme.

There are other display characteristics which contribute to the conspicuousness of the crab and which are attained most fully in those species in which waving is highly developed. These characteristics include faster tempo of the wave, a rhythm accented by jerks or other specializations and an increase in time devoted daily to waving.

The trend toward the attraction of females to the male burrow, typical of the broad-fronts, may well have adaptive value, since pairs copulating at the surface are fully exposed to predation by birds. A probable factor in the evolution of this pattern is the fact that among broad-fronts the male is often considerably larger than the female. Because of this size discrepancy males cannot easily descend into the narrow burrows of the females.

Many species with highly developed displays resemble primitive forms when waving at low intensity. This is especially well shown when a crab is feeding and waving at the same time, when tidal or meteorological conditions are unfavorable, or when the crab is not physiologically in full display condition. Under any of these circumstances even species as far apart phylogenetically as *maracoani, stenodactyla* and *lactea* may raise the cheliped only slightly and lower it in the same, nearly vertical plane, scarcely elevating the body. This low intensity display therefore is very similar to the full display of *rhizophorae, manii* and their relations.

There appear to be no structural reasons preventing vertical wavers from displaying in the lateral fashion. The form of the condyles, the proximal concavities of articulating segments and the elasticity of the connections are similar throughout, although Peters (1955, pp. 489 ff.) illustrates minor differences in the degrees of possible motion in two closely related species. Throughout the genus the cheliped is often widely extended, regardless of the type of wave performed during display, in combat between males when the chelae of the combatants are actually engaged.

Altevogt (1955.2, p. 514) recorded differences in the display of very large and moderate-sized individuals of *marionis,* the giants having a less out-reaching form. He thinks this is probably associated with the altered center of gravity. It seems to the present investigator that the evolution of the form of display in the gigantic species of neotropical narrow-fronts, *maracoani* and *insignis,* may have been guided by similar problems of weight and balance.

Evidence has recently been found that displacement behavior sometimes occurs during *Uca* display, and it seems likely that such behavior varies among the species roughly in accordance with their phylogenetic position. Gordon (1955) first reported displacement feeding (in the sense in which the term has been used by Armstrong, 1950, and Tinbergen, 1952) in a number of African species. I fully agree with her interpretation, having often observed similar types of activity not only in *Uca* but in other genera of displaying ocypodids, notably *Ilyoplax.*

Gordon's observations were of feeding, often in a token, non-functional fashion, usually after fighting or after high intensity display and a thwarting of mating behavior.

The current studies present evidence of two more aspects of the subject. First, displacement behavior is most prevalent in species characterized by highly developed display. Second, in these species there occurs not only displacement feeding, as described by Gordon, but also displacement claw-cleaning. The large manus and chelae are buffed and polished by the small, or at least the requisite motion is made, although the terminal brush may not actually touch the large chelae. The gesture is repeated frequently even though the crab has been above ground for many minutes and the cheliped is altogether free of mud. This activity seems to occur especially when there is conflict between the urge to display and that to escape, such as when the camera or observer is very close to the crab.

Current observations indicate furthermore that there will prove to be specific differences in the tendency toward one type or another of displacement behavior. For example, *festae* in Ecuador, *deichmanni* in Panama and *cumulanta* in Trinidad and Venezuela all appear to be especially prone to displacement claw-cleaning. *U. lactea* in the Indo-Pacific and *leptodactyla* in Brazil, on the other hand, seem to have a stronger tendency to displacement feeding. In contrast, in the primitive Indo-Pacific narrow-fronts (*rhizophorae et al.*) no displacement behavior has been noticed; it appears likely that in these

TABLE 1. SPECIES OF *Uca* IN WHICH DISPLAY HAS BEEN STUDIED DURING THE PRESENT INVESTIGATION

Note: The majority of these forms are undoubtedly good species. It is expected that some will be reduced to subspecific rank, especially certain narrow-fronted crabs with narrow ranges in the Indo-Pacific. This however does not alter the fact that the displays of all the forms listed below are distinct.

The 43 species are arranged alphabetically since a phylogenetic presentation must await the publication of correlated morphological evidence. Display has also been observed in at least ten additional species; since these are apparently new and undescribed, they have been omitted from the list. Motion picture records have been obtained of more than three-quarters of all the species observed.

In the second column are given references to descriptions of waving published after 1940. An account of earlier work on *Uca* display is given in Crane, 1941, p. 152. Since these early reports lacked a comparative ethological viewpoint they remain, for present purposes, chiefly of historical interest and will not be repeated here. The only references included below, therefore, are recent wave descriptions which are to some degree specifically diagnostic. Published records which are extremely incomplete (e.g. of *minax*, Crane, 1944) are omitted, as are displays not described but mentioned in connection with another subject (e.g. Gordon, 1955, on displacement behavior).

In addition to the displays listed below which Peters (1955) has also recorded, he has described (*loc. cit.*) those of *macrodactyla glabromana* Bott and *leptochela* Bott, neither of which species has been observed by the present author. Hediger (1934) gives a helpful account of *tangeri* in a reference inadvertently omitted by Crane, 1941.

Species	Description of waving since 1940	General Range	Localities where display was observed by author
annulipes (Latreille)	—	Indo-Pacific	Pakistan (Karachi), Ceylon, Penang, Singapore, Sarawak, Philippines
batuenta Crane	Crane, 1941 Peters, 1955	E. Pacific	Panama, Ecuador
beebei Crane	Crane, 1941 Peters, 1955	E. Pacific	Panama, Ecuador
cumulanta Crane	Crane, 1943	W. Atlantic	Venezuela, Trinidad
deichmanni Rathbun	Crane, 1941	E. Pacific	Panama
dussumieri (Milne Edwards)	—	Indo-Pacific	Singapore, Sarawak, Philippines
festae Nobili	—	Ecuador	Ecuador
gaimardi (Milne Edwards)	—	Western & Central Pacific	French Oceania (Tahiti, Raiateia, Bora Bora)
galapagensis Rathbun	—	E. Pacific	Ecuador
heterochelos (Lamarck)	—	W. Atlantic	Venezuela
heteropleura (Smith)	Crane, 1941	E. Pacific	Panama, Ecuador
inaequalis Rathbun	Crane, 1941 Peters, 1955	E. Pacific	Panama, Ecuador
insignis (Milne Edwards)	—	E. Pacific	Panama, Ecuador
inversa (Hoffmann)	—	Indo-Pacific	Pakistan (Karachi)
ischnodactyla Nemec	—	Fiji	Fiji
lactea (de Haan)	—	Indo-Pacific	Pakistan (Karachi), Singapore, Philippines, Fiji, Samoa
latimana (Rathbun)	Crane, 1941 Peters, 1955	E. Pacific	Panama, Ecuador
leptodactyla (Guérin)	—	W. Atlantic	Venezuela, Brazil
limicola Crane	—	E. Pacific	Panama
longidigitum (Kingsley)	—	E. Australia	Nr. Brisbane

TABLE 1. SPECIES OF *Uca* IN WHICH DISPLAY HAS BEEN STUDIED DURING THE PRESENT INVESTIGATION *(Continued)*

Species	Description of waving since 1940	General Range	Localities where display was observed by author
manii Rathbun	—	Indo-Pacific	Singapore
maracoani (Latreille)	Crane, 1943	W. Atlantic	Venezuela, Trinidad, British Guiana, Surinam, Brazil
marionis (Desmarest) (incl. *nitida* (Dana))	Altevogt, 1955.1, 1955.2	Indo-Pacific	Singapore, Sarawak, East & North Australia, Philippines, Fiji
minax (Le Conte)	—	W. Atlantic	New Jersey
mordax (Smith)	Beebe, 1928 Crane, 1943	W. Atlantic	Guatemala, Venezuela, Trinidad, Brazil
oerstedi Rathbun	Crane, 1941	E. Pacific	Panama
olympioi Oliveira	—	S. Brazil	Rio de Janeiro
panamensis (Stimpson)	—	E. Pacific	Panama
princeps (Smith)	Crane, 1941 Peters, 1955	E. Pacific	Panama, Ecuador
pugilator (Bosc)	Crane, 1944 Burkenroad, 1947	W. Atlantic	Connecticut, New York, Florida
pugnax (Smith)	Crane, 1944	W. Atlantic	Massachusetts, Connecticut, New York, Florida
pugnax rapax (Smith)	Crane, 1943	W. Atlantic	S. Florida, Guatemala, W. Indies, Colombia, Venezuela, British Guiana, Surinam, Brazil
rathbunae Pearse	—	Philippines	Manila, G. of Davao
rhizophorae (Tweedie)	—	Malaya & Borneo	Singapore, Sarawak
rosea (Tweedie)	—	Malaya	Penang
saltitanta Crane	Crane, 1941 Peters, 1955	E. Pacific	Panama
signata (Hess)	—	Indo-Pacific	Australia (Gladstone), Philippines
speciosa (Ives)	—	W. Atlantic	S. Florida
stenodactyla (Milne Edwards & Lucas)	Crane, 1941 Peters, 1955	E. Pacific	Costa Rica, Panama, Ecuador
stylifera (Milne Edwards)	Crane, 1941	E. Pacific	Panama, Ecuador
terpsichores Crane	Crane, 1941	E. Pacific	Panama, Ecuador
tetragonon (Herbst)	—	Indo-Pacific	French Oceania (Bora Bora)
thayeri Rathbun	—	W. Atlantic	Trinidad, Brazil
zamboangana Rathbun	—	Philippines	Gulf of Davao

species display is so feebly developed that, when any conflict or frustrating situation arises, the crab simply stops waving.

No comment can yet be made on the role displacement behavior, through ritualization, may have played in the evolution of display motions.

Studies on heliconiid butterflies in Trinidad (Crane, 1955 and in ms.) apparently show conclusively the frequent occurrence of displace-

TABLE 2. ARRANGEMENT OF *Uca* SPP. ACCORDING TO GENERAL TYPE OF WAVE.

Key: Species names in *italics*: narrow-fronts. Species names in **bold-face:** broad-fronts.

IP: Indo-Pacific.
EP: Eastern Pacific.
WA: Western Atlantic.

curtsy, rapping, special steps } general type of outstanding characteristic in advanced display.

No AD: No special advanced display characteristics.

(Where distribution symbol is not followed by one of these key designations, advanced display is incompletely known. See text).

Body position at moderate display intensity	Wave Vertical (Cheliped raised upward at beginning of wave; always returned to position in same plane)	Wave Lateral (Cheliped extended to side at beginning of wave; often returned to position via a circular route)
Body raised throughout a series of waves	*zamboangana* (IP)	**annulipes** (IP) (curtsy) **beebei** (EP) (special steps) **festae** (EP) (special steps) **galapagensis** (EP) **inversa** (IP) **lactea** (IP) (curtsy) **latimanus** (EP) (curtsy) **leptodactyla** (WA) (curtsy) **limicola** (EP) **minax** (WA) **mordax** (WA) (curtsy) **olympioi** (WA) (curtsy) **pugnax** (WA) (curtsy) **stenodactyla** (EP) (special steps) **terpsichores** (EP) (special steps) *insignis* (EP) (special steps) *maracoani* (WA) (special steps) *princeps* (EP) *stylifera* (EP) (special steps)
Body conspicuously raised and lowered with each wave.	*dussumieri* (IP) (No AD) *marionis* (IP) (No AD) *signata* (IP) (No AD) **thayeri** (WA) (No AD)	**batuenta** (EP) (rapping) **cumulanta** (WA) (rapping) **deichmanni** (EP) (rapping) **inaequalis** (EP) (rapping) **oerstedi** (EP) **panamensis** (EP) **pugilator** (WA) (rapping) **saltitanta** (EP) (rapping) **speciosa** (WA) (rapping) *heterochelos* (WA) *heteropleura* (EP) (No AD)
Body not raised, at all, or minimally raised and lowered with each wave.	**gaimardi** (IP) (No AD) *longidigitum* (Australia) *tetragonon* (IP) (No AD) *ischnodactyla* (IP) (No AD) *manii* (IP) (No AD) *rathbunae* (IP) (No AD) *rhizophorae* (IP) (No AD) *rosea* (IP) (No AD)	

ment behavior in these insects. Its probable occurrence has been mentioned in salticid spiders (*idem,* 1948, p. 202), mantids (*idem,* 1952, p. 288) and *Drosophila* (Bastock & Manning, 1955, p. 104). It now seems likely that displacement behavior will prove to be a noteworthy factor in the ethological study of many higher invertebrates.

VIII. Summary

Two basic patterns of display have been distinguished during field studies of more than fifty species of fiddler crabs (*Uca*). The first pattern is characteristic of a group of species with narrow fronts. It is distinguished by a simple, more or less vertical gesture ("wave") made with the major cheliped of the male, and by the male's pursuit of the female toward her burrow; copulation in the known instances takes place on the surface of the ground. The second pattern is typical of broad-fronted species in the genus. It is characterized as follows: the cheliped is unflexed laterally, rather than vertically elevated, and sometimes completes a circular motion in returning to rest position; there is in addition a distinct second stage of display which is usually elicited by the approach of a female and which depends both on special movements of the various appendages and on an increased tempo of waving; finally, in the last stage of display the male attracts the female down his own burrow, which he enters first. A few species with intermediate types of behavior have been observed, especially in the Indo-Pacific.

The simplest and most primitive of the narrow-fronted displays are found in a group of closely related Indo-Pacific species of narrow distribution which inhabit protected estuaries and tidal streams; *manii* and *rathbunae* are examples. Displays of higher development are found among species inhabiting more saline, exposed locations; typical of these are *tetragonon* and *zamboangana,* both from the Indo-Pacific area. The narrow-fronted crabs reach their highest display development, along with their greatest morphological specialization, in the neotropical representatives, culminating in *insignis* and *maracoani.* All favor relatively exposed habitats.

The broad-fronted, laterally waving fiddler crabs are distributed in both the Indo-Pacific and American regions but, unlike the narrow-fronted species, they are poorly represented in the Indo-Pacific. As in the other groups, the highest display development occurs among species living in more seaward niches. Representatives are found of both simple and highly evolved displays. As examples, *gaimardi,* from the western and central Pacific, illustrates the simplest known type of lateral display, while complex specializations are shown variously by *lactea* from the Indo-Pacific, *saltitanta* and *terpsichores* from the eastern Pacific and *pugnax* from the western Atlantic.

Three wide-ranging Indo-Pacific species have been observed in display over distances ranging from 5,000 to 8,000 miles. No gross intraspecific differences were noted on the peripheries or elsewhere in their ranges, except that some displaying *lactea* built small structures of sandy mud in Karachi, but not in either the Philippines or the Fiji Islands, at least during the period of observation.

As is usual in a number of animals, the general trend in display evolution in *Uca* is toward increased conspicuousness. This increase is attained principally by higher speed in waving, by greater complexity in the rhythms and forms of display motions and by increased apparent size, through extension of the appendages either vertically or horizontally. The species in which display is highly evolved also spend a greater portion of their time in display than do other members of the genus.

Displacement behavior during *Uca* display is briefly discussed, including its possible role in the systematics of the group.

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EXPLANATION OF THE PLATE

Plate I

Oblique views of different types of wave in fiddler crabs. For comparison with frontal views, Text-figs. 1 and 3.

Fig. 1. Vertical wave: *Uca dussumieri* displaying near Sasa, Gulf of Davao, Philippine Islands. Maximum elevation of cheliped.

Fig. 2. Vertical wave: *Uca marionis* in Singapore. Major cheliped partially elevated. Note forward direction of merus and carpus, and compare their position in Fig. 4, below.

Fig. 3. Lateral wave: *Uca latimanus* near Panama City, Panama. Maximum elevation of cheliped.

Fig. 4. Lateral wave: *Uca annulipes* near Santobong, Sarawak. Cheliped partially elevated. Note lateral direction of merus and carpus.